Translocations and the Preservation of Allelic Diversity

CRAIG A. STOCKWELL,*§ MARGARET MULVEY,† AND GARY L. VINYARD‡

*Program in Ecology, Evolution and Conservation Biology, and Biological Resources Research Center, Department of Biology, University of Nevada, Reno, NV 89557, U.S.A.
†Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29802, U.S.A.
‡Department of Biology, University of Nevada, Reno, NV 89557, U.S.A.

Abstract: *Translocation is a tool commonly used for the conservation of threatened and endangered fish species. Despite extensive use, the biological implications of translocation remain poorly understood. Of particular interest is the effect of translocation on genetic variability. Maintenance of genetic variability in these "refuge" populations is assumed to be important for both short- and long-term success. We examined allozyme variability at 16 loci for western mosquitofish (*Gambusia affinis*) populations with known histories of introduction. Refuge populations had significantly lower levels of heterozygosity. Refuge populations also had considerably lower levels of allelic diversity than parental populations. All losses were of relatively rare alleles (frequency less than 0.1 in parental population). These losses were probably due to an undocumented bottleneck early in the introduction history. These results were surprising because the initial transplant involved 900 fish and because mosquitofish have numerous reproductive traits that should minimize the effects of bottlenecks on genetic diversity. A literature review revealed that genetic variability is often reduced in refuge populations and that such reductions typically involve the loss of alleles. We suggest that translocated populations be examined periodically for losses of genetic variability.*

Translocaciones y la Preservación de la Diversidad Alélica

Resumen: *Una herramienta conservacionista utilizada comúnmente es la translocación de especies de peces amenazadas y en peligro. A pesar de su uso extensivo, las implicaciones biológicas de las translocaciones han sido poco entendidas. El efecto de la translocación sobre la variabilidad genética es de particular interés. Se asume que el mantenimeinto de la variabilidad genética en estas poblaciones "refugio" es importante para su éxito a corto y largo plazo. Examinamos la variabilidad de alozimas en 16 loci en poblaciones de* Gambusia affinis *con introduccion conocidas. Las poblaciones refugio tuvieron niveles de heterocigosidad significativamente menores. Las poblaciones refugio también presentaron niveles de diversidad alélica considerablemente menores a las de las poblaciones parentales. Todas las pérdidas fueron de alelos relativamente raros (frecuencia menor a 0.1 en población parental). Estas pérdidas probablemente se debieron a un cuello de botella no documentado en el historial de introducción. Estos resultados fueron sorprendentes porque el transplante inicial involucró 900 peces y porque la especie tiene numerosas características reproductivas que debieran minimizar los cuellos de botella sobre la diversidad genética. Una revisión de literatura reveló que la variabilidad genética en poblaciones refugio a menudo es reducida, y que tales reducciones típicamente involucran la pérdida de alelos. Sugerimos que las poblaciones translocadas sean examinadas periódicamente para detectar pérdidas de variabilidad genética.*

§ *Current address: Savannah River Ecology Laboratory, Drawer E, Aiken 29802, U.S.A., email stockwell @srel.edu*
Paper submitted December 15, 1994; revised manuscript accepted August 3, 1995.

Introduction

For threatened and endangered species with restricted distributions, conservation biologists often face problems that require direct intervention. One conservation strategy used to lessen the threat of extinction is the translocation of animals to new localities to establish additional populations (Griffith et al. 1989). More than 80% of recovery plans for threatened and endangered fish species call for the use of translocation as a conservation tool (Williams et al. 1988). In the desert southwest of the United States, newly established fish populations may be referred to as "refugia" (Turner 1984; Echelle 1991; Hendrickson & Brooks 1991).

Despite the extensive use of translocation, the biological implications of this practice remain poorly understood (Hendrickson & Brooks 1991). Of particular interest is whether genetic variability is reduced in the newly established refuge populations. Loss of genetic variability is especially likely when an effectively small number of individuals is used to found refuge populations (Wright 1931; Nei et al. 1975).

Low effective population sizes (N_e) can occur even when census estimates are large (Briscoe et al. 1992). Differences between census number and N_e can be due to factors that increase the variance in reproductive success among individuals (Wright 1931; Lande & Barrowclough 1987). Populations of small size are vulnerable to loss of genetic variability due to genetic drift and/or inbreeding (Wright 1931).

Conservation biologists routinely use allozyme electrophoresis to assess genetic variability in terms of overall heterozygosity, number of polymorphic loci, and the number of alleles per locus. These measures may yield different patterns, however (Allendorf 1986; Leberg 1992). Allele loss is most strongly influenced by bottleneck size (Nei et al. 1975; Allendorf 1986); smaller bottlenecks produce greater losses. Loss of alleles can be of special concern because even the loss of a rare allele can reduce future evolutionary potential (Allendorf 1986). Heterozygosity is influenced by bottleneck size and duration; bottlenecks of short duration have little predicted effect on heterozygosity (Nei et al. 1975). Loss of heterozygosity has been of general concern because of its potential effects on fitness (Mitton & Grant 1984; Allendorf & Leary 1986). Reduced fitness of individuals can lead to reductions in rate of population growth (Leberg 1990) and thus increase the probability of population extinction.

Because of its importance, many conservation plans call for the maintenance of genetic variability in translocated populations (Vrijenhoek et al. 1985; Allendorf & Leary 1988; Quattro & Vrijenhoek 1989). Numerous studies have described genetic variability in hatchery populations of fish (for review see Allendorf & Ryman 1987), but studies examining genetic variability of translocated populations of fish in the wild are lacking (but see Turner 1984; Scribner et al. 1992).

Mosquitofish (*Gambusia affinis* and *G. holbrooki*) provide an excellent opportunity to examine the effects of translocation on genetic variability because introduction histories can be reconstructed. Also, mosquitofish have two life-history traits that should minimize the loss of genetic variability in translocated populations. First, mosquitofish have high reproductive potential (Krumholz 1948; Leberg 1993), so bottleneck durations should be short. Second, because female mosquitofish retain sperm and commonly have multiply sired broods (Chesser et al. 1984; Robbins et al. 1987), ratios of N_e to N should be maximized (Sugg & Chesser 1994). For a series of western mosquitofish populations with known histories of introduction, we examine the null hypothesis that genetic variability does not differ between introduced populations and their parental stocks.

In 1922, 600 mosquitofish (*G. affinis*) from the vicinity of Austin, Texas, and 300 fish from the vicinity of Hearne, Texas, were introduced to Fort Sutter lily pond in northern California (Fig. 1; Lenert 1923). By the following year mosquitofish from Fort Sutter had been

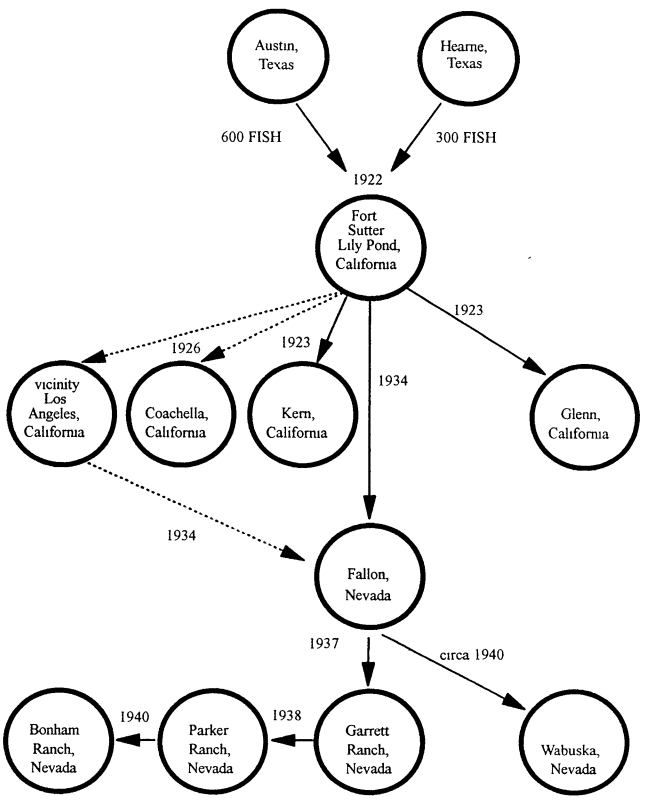

Figure 1. Introduction history for selected populations of western mosquitofish in California and Nevada. Solid lines indicate introductions that have been well documented. Dotted lines indicate likely introduction scenarios.

used to establish seven "hatcheries" throughout California (Fig. 1; Lenert 1923). In 1923 fish were translocated from Fort Sutter to the Oroville "hatchery." These fish were subsequently distributed throughout Glenn County, California (Lenert 1923). In 1923 mosquitofish were transplanted from Fort Sutter to the Bakersfield "hatchery" and subsequently distributed throughout Kern County. No subsequent introductions into this county are documented (Dick Meyer, personal communication). In 1926 mosquitofish were imported to Coachella Valley. Although their immediate ancestors were not documented, they were likely descendants of the Fort Sutter population. No additional introductions are known to have occurred at these sites.

In 1934 mosquitofish were introduced to Fallon, Nevada, from Fort Sutter and from the vicinity of Los Angeles (La Rivers 1962; V. Mills, personal communication). Mosquitofish were introduced from Fallon to Wabuska Hot Springs in the late 1930s by Wally White (V. Mills & R. Alcorn, personal communication). In 1937 mosquitofish were introduced from Fallon to Garrett Ranch in the Black Rock Desert (J. Parker, personal communication). By 1940 mosquitofish had been introduced from Garrett Ranch to the Parker Ranch (northern Smoke Creek Desert) and from the Parker Ranch to the Bonham Ranch (southern Smoke Creek Desert) (J. Bonham, J. Parker, & B. Paschall, personal communication). These Nevada mosquitofish populations are at least 50 linear kilometers apart, and no natural gene flow occurs.

Methods

An evaluation of the consequences of translocation on genetic variation in refugia requires genetic data from the source population as well as from refuge populations. The Fort Sutter mosquitofish population was the source for all of the refuge populations evaluated in this study (Fig. 1). Unfortunately, the Fort Sutter lily pond was drained in 1991. To reflect the genetic composition of the source population, we constructed a hypothetical "1922 Fort Sutter" population. Because the population was founded with 600 fish from Austin and 300 fish from Hearne, we used a weighted mean of allele frequencies for these two Texas populations to estimate the allele frequencies for the Fort Sutter population. Further, these Fort Sutter allele frequencies were used to estimate Hardy-Weinberg heterozygosity for each locus in the Fort Sutter population. The total number of alleles at Fort Sutter was estimated as the sum of all alleles from Austin and Hearne.

Fish were collected from the little Brazos near Hearne, Texas, and from Waller Creek, a tributary of the Colorado River near Austin, Texas (Fig. 1). Three California populations were sampled: Kern, Glenn, and Coachella Valley (Fig. 1). Five Nevada populations were sampled: Fallon, Wabuska, Garrett, Parker, and Bonham (Fig. 1). All fish were collected during the fall of 1993.

Approximately 40 fish per population were prepared for allozyme electrophoresis following methods outlined by McClenaghan et al. (1985). Buffers and corresponding protein systems included continuous tris citrate (pH 8.0; Selander et al. 1971) for aconitase hydratase (Acoh-A, EC 4.2.1.3), glycerol-3-phosphate dehydrogenase (G3pdh-A; EC 1.1.1.8), creatine kinase (Ck-A, B; EC 2.7.3.2), glucose-6-phosphate isomerase (Gpi-B; EC 5.3.1.9), isocitrate dehydrogenase (Idh-A; EC 1.1.1.42), mannose-6-phosphate isomerase (Mpi-A; EC 5.3.1.8), phosphogluconate dehydrogenase (Pgdh-A; EC 1.1.1.44), and phosphoglucomutase (Pgm-A; EC 5.4.2.2); and discontinuous tris citrate (buffer C- Ayala et al. 1972) for fumerate hydratase (Fumh-A; EC 4.2.1.2), L-lactate dehydrogenase (Ldh-A, B; EC 1.1.1.27), malate dehydrogenase (Mdh-A, B; EC 1.1.1.37), malate dehydrogenase($NADP^+$) (Mdhp-B; EC 1.1.1.40), and purine nucleoside phosphorylase (Pnp-A; EC 2.4.2.1).

The most common allele was designated "100" and the other alleles were scored according to their mobility relative to the common allele. Standard samples were used on all gels for comparisons between populations. We used BIOSYS-1 (Swofford & Selander 1981) to calculate allele frequencies, percent polymorphic loci (99% criterion; P), mean heterozygosity (H), and the mean number of alleles per locus (A). Number of alleles per locus was estimated for loci that were polymorphic in at least one population. Departure from Hardy-Weinberg expectations was tested by chi-square analyses. (Tests in which the expected number of any genotype classes was less than three were not reported.)

We assessed genetic variability in terms of H, P, and A (Leberg 1992). Two methods were used to examine the effects of translocation on genetic variability as measured by these indices. First, we used one-tailed t tests to compare the genetic variability for the eight refuge populations in Nevada and California to genetic variability in the two natural populations in Texas. Second, we used one-tailed paired t tests to compare refuge populations to their respective parental populations. Effects of serial translocations were examined by regressing heterozygosity on the number of translocations though which a population had passed.

Results

Eleven of 16 loci were polymorphic, but only 3 loci were polymorphic in all 10 populations (Table 1). Five loci were monomorphic in all populations: Ck-A, Ck-B, Ldh-A, Mdh-A, Mdh-B.

Estimates of expected Hardy-Weinberg heterozygosity and direct-count heterozygosity were significantly correlated ($r = 0.953$; $F_{[1,8]} = 77.547$; $p < 0.001$), and we re-

Table 1. Allele frequencies for 10 sampled mosquitofish populations and the reconstructed Fort Sutter population.

	Population										
	Austin	*Hearne*	*Coachella*	*Glenn*	*Kern*	*Fallon*	*Garrett*	*Parker*	*Bonham*	*Wabuska*	*Fort Sutter*[a]
Locus											
Fumh-A											
125										0.068	
100	1.000	0.688	0.256	0.675	0.397	0.615	0.550	0.423	0.500	0.932	0.896
61		0.313	0.744	0.325	0.603	0.385	0.450	0.577	0.500		0.104
n	40	40	39	40	39	39	40	39	35	37	
Ldh-B											
100	0.962	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.975
78	0.038										0.025
n	40	40	40	40	39	39	40	40	40	37	
Mdhp-B											
128	0.417	0.149	0.355	0.077	0.051	0.230	0.438	0.448	0.414	0.422	0.328
100	0.583	0.851	0.645	0.923	0.949	0.770	0.563	0.552	0.586	0.578	0.672
n	36	37	38	39	39	37	40	29	29	32	
Pnp-A											
100	0.934	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.924	0.956
83	0.066									0.076	0.044
n	38	40	38	40	39	34	39	40	40	33	
Acoh-A											
124	0.297		0.150			0.026			0.029	0.013	0.198
100	0.578	0.962	0.850	1.000	0.949	0.974	1.000	0.948	0.971	0.974	0.706
90	0.125	0.038			0.051			0.052		0.013	0.096
n	32	39	40	38	39	39	40	29	35	39	
G3pdh-A											
141	0.475	0.184	0.167	0.171	0.115	0.243	0.262	0.289	0.359	0.694	0.378
100	0.525	0.816	0.833	0.829	0.885	0.757	0.738	0.711	0.641	0.306	0.622
n	40	38	30	38	30	35	40	38	32	31	
Gpi-B											
100	0.795	0.897	0.925	1.000	0.910	1.000	1.000	1.000	1.000	0.910	0.829
56	0.205	0.103	0.075		0.090					0.090	0.171
n	39	39	40	40	39	39	39	40	40	39	
Idh-A											
100	0.938	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.959
93	0.063										0.042
n	40	40	33	40	39	34	38	34	36	39	
Mpi-A											
109	0.038										0.025
100	0.900	0.833	0.850	0.712	0.859	0.838	0.750	0.837	0.797	0.941	0.878
89					0.013						
82	0.063	0.167	0.150	0.287	0.128	0.162	0.250	0.162	0.203	0.059	0.098
n	40	39	40	40	39	37	38	40	32	34	
Pgdh-A											
115	0.075	0.150	0.066	0.125	0.056						0.100
100	0.925	0.813	0.934	0.875	0.944	1.000	1.000	1.000	1.000	1.000	0.888
88		0.038									0.013
n	40	40	38	40	36	39	39	39	40	39	

Table 1. Continued.

	Population										
	Austin	*Hearne*	*Coachella*	*Glenn*	*Kern*	*Fallon*	*Garrett*	*Parker*	*Bonham*	*Wabuska*	*Fort Sutter*[a]
Locus											
Pgm-A											
100	0.865	0.975	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.902
82	0.135	0.025									0.098
n	37	40	34	40	39	33	40	31	32	39	
Alleles per locus[b]	2.09	1.82	1.64	1.45	1.73	1.45	1.36	1.45	1.45	1.73	2.27
Mean heterozygosity[c]	0.172 (0.052)	0.104 (0.034)	0.122 (0.041)	0.089 (0.038)	0.074 (0.026)	0.098 (0.044)	0.115 (0.052)	0.094 (0.040)	0.120 (0.055)	0.081 (0.034)	0.241[a]
Number of translocations	0	0	2	2	2	2	3	4	5	3	1

[a] *Allele frequencies were estimated as a weighted mean of Austin and Hearne populations. These estimated allele frequencies were then used to estimate Hardy-Weinberg heterozygosity.*
[b] *Estimates are based on 11 polymorphic loci listed above. A locus was considered polymorphic if more than one allele was detected in at least one population.*
[c] *Estimates are based on 11 polymorphic loci listed above and 5 monomorphic loci: Mdh-A, Mdh-B, Ck-A, Ck-B, and Ldh-A. Standard errors are in parentheses.*

port only direct-count heterozygosity values. Alleles per locus and percent polymorphic loci were significantly correlated ($r = 0.992$; $F_{[1,8]} = 517.484$; $p < 0.001$). Therefore, we report only alleles per locus. Mean number of alleles per locus and direct-count heterozygosity were not significantly correlated ($r = 0.464$; $F_{[1,8]} = 2.189$; $p = 0.177$).

Only 1 of 20 comparisons revealed a significant departure of allele frequencies from Hardy-Weinberg expectations; this result was expected by chance. Significant deviation from Hardy-Weinberg expectations occurred for Fumh-A in the Parker population.

Our assumption that fish from both Texas populations successfully reproduced and served as founders for the series of populations surveyed in this study is supported by the allozyme data. Each Texas population has at least one allele not shared by the other Texas population but represented in refuge populations (Hearne, Fumh-A^{61}; Austin, Acoh-A^{124}, Pnp-A^{83}).

Heterozygosity was significantly lower in the refuge populations than in the natural populations ($t = 2.048$, df = 8, $p = 0.038$; Table 1). An analysis of all translocations revealed a significant reduction in heterozygosity between refuge populations and their respective parental populations ($t = 2.517$; df = 7; $p = 0.02$), but the number of translocations (Table 1) had no significant effect on population heterozygosity ($r = 0.351$, $F_{1,6} = 0.842$, $p = 0.394$).

Allelic diversity was considerably reduced among all refuge populations compared to the two Texas parental populations ($t = 3.579$, df = 8, $p < 0.004$). The hypothetical Fort Sutter population had 2.27 alleles per locus, whereas the number of alleles per locus in the eight refuge populations varied from 1.36 to 1.73 (Table 1); a 24–40% reduction in allelic diversity. Refuge populations had significantly lower allelic diversity than their respective parental populations ($t = 2.071$, df = 7, $p = 0.039$). Most lost alleles were relatively rare.

Six alleles estimated to occur in the Fort Sutter population were lost in all four populations founded from the Fort Sutter population (Idh^{93}, Ldh-B^{78}, Mpi-A^{109}, Pnp-A^{83}, Pgdh-A^{88}, and Pgm-A^{82}). Some refuge populations had higher allelic diversity than their parental source. The apparent losses and gains in these populations do not seem to follow any consistent pattern. For instance, Acoh-A^{90} is lost and regained on two occasions. In all cases Acoh-A^{90} was at low frequency, which suggests that such apparent losses and gains could be due to sampling error.

Discussion

Because of their life-history traits, mosquitofish should provide a best-case scenario for the preservation of genetic diversity in translocated populations. Earlier work has shown mosquitofish to retain variability during founding events (Brown 1987; Scribner et al. 1992). Historical records show that 900 mosquitofish were introduced to Fort Sutter. Genetic variability in such a large population should have been maintained, but we detected a significant reduction in genetic variability.

Although heterozygosity was significantly lower in refuge populations, it is noteworthy that heterozygosity in three of the refuge populations exceeded the heterozygosity in one of the natural populations (Hearne; Table 1). Also, there was no relationship between heterozygosity and the number of bottlenecks through which a population passed.

Table 2. The effects of translocation events on allelic diversity and heterozygosity.

Species	*Allelic diversity*	*Heterozygosity*	*Translocation type*[a]	*Reference*[b]
Black seabream *Acanthopagrus schlegeli*	reduced	reduced	hatchery	Taniguchi et al. 1983
Cutthroat trout *Oncorbynchus clarki*	reduced	reduced	hatchery	Allendorf & Phelps 1980
Atlantic salmon *Salmo salar*	—	reduced	hatchery	Ståhl 1983
Atlantic salmon	reduced[c]	reduced[c]	hatchery	Cross & King 1983
Atlantic salmon	no[d]	reduced	hatchery	Verspoor 1988
Atlantic salmon	reduced	reduced	hatchery	Kolijonen 1989
Atlantic salmon		no	hatchery[e]	Crozier & Moffett 1989
Brook trout *S. trutta*	reduced	—	hatchery	Ryman & Ståhl 1980
Brook trout	reduced	reduced	hatchery	Vuorien 1984
Pecos gambusia *G. nobilis*	no[f]	no	hatchery	Edds & Echelle 1989
Leon Springs pupfish *Cyprinodon bovinus*	no[f]	no	hatchery	Edds and Echelle 1989
Comanche Springs pupfish *Cyprinodon elegans*	no[f]	no	hatchery	Edds & Echelle 1989
Colorado squawfish *Ptychocheilus lucius*	no	no	hatchery	Ammerman & Morizot 1989
Western mosquitofish *Gambusia affinis*	reduced	no	Hawaii	Scribner et al. 1992
Desert pupfish *Cyprinodon macularius*	no	no	refugia	Turner 1984
Anolis lizard *Anolis grahami*	reduced	no	Bermuda	Gorman et al. 1978; Taylor & Gorman 1975
Anolis lizard *A. aenus*	reduced	no	Trinidad	Gorman et al. 1978
Anolis lizard *A. trinitatis*	reduced	reduced	Trinidad	Gorman et al. 1978
Anolis lizard *A. extremus*	reduced	reduced	St. Lucia	Gorman et al. 1978
A. extremus	reduced	reduced	Bermuda	Gorman et al. 1978
Anolis lizard *A. leachi*	reduced	reduced	Bermuda	Gorman et al. 1978
House Sparrow *Passer domesticus*	reduced	no	Australia	Parkin & Cole 1985
House Sparrow	reduced	reduced	New Zealand	Parkin & Cole 1985
Common Myna *Acridotheres tristis*	reduced	no	Hawaii	Baker & Moeed 1987; Fleischer et al. 1991
Common Myna	reduced	no	Australia	Baker & Moeed 1987
Common Myna	reduced	reduced	South Africa	Baker & Moeed 1987
Common Myna	reduced	no	Fiji	Baker & Moeed 1987
Common Myna	no	no	New Zealand	Baker & Moeed 1987
Reindeer *Rangifer tarandus*	reduced[g]	reduced[g]	Iceland	Roed et al. 1985

[a] *The locality of the established population is given in cases in which these populations were established in the wild. Also included are populations established in artificial refugia and hatchery stocks that were derived from parental wild stocks.*
[b] *A literature survey was conducted using two data bases (M. W. Smith et al. 1982; M. H. Smith et al. 1994). We searched for papers that examined allozyme variation in translocated populations of vertebrates.*
[c] *The authors reported a reduction, although the differences were not statistically significant.*
[d] *Monomorphic loci were significantly more common in hatchery populations than in wild samples.*
[e] *These hatchery stocks are regularly outcrossed with wild stocks.*
[f] *Authors note the loss of rare alleles.*
[g] *Estimates are based on one highly polymorphic locus.*

The most striking result was a reduction in allelic diversity in refuge populations that varied from 24% to 40%. Most notable was the loss of six alleles in four populations founded from Fort Sutter. Sampling error probably does not account for absence of alleles in the refuge populations because approximately twice as many alleles were sampled in the initial refuge populations (Kern, Coachella, Fallon, and Glenn) as in the parental

populations in Texas. It is unlikely that all six alleles were lost four different times. It is more likely that these alleles were not present in the Fort Sutter population when translocations to other sites were initiated.

We hypothesize that the loss of rare alleles occurred during a bottleneck early in the establishment of the Fort Sutter population. The probability of retaining rare alleles has been shown to be directly related to effective population size (Allendorf 1986). A comparison of our data to the predictions of this model suggests that a severe bottleneck of less than 10 individuals would be necessary to produce the loss of alleles we observed. A population crash during early establishment seems likely for two reasons. First, mosquitofish may have been stressed during translocation. Early attempts to establish populations of mosquitofish in northern climates met with mixed success (Krumholz 1948). Second, western mosquitofish were translocated from Fort Sutter to seven other sites within the next year (Lenert 1923). If a bottleneck occurred, it must have happened early in 1922 so that the population could grow to a size sufficient to sustain seven translocations within the next year.

An alternative interpretation of our data is that alleles currently missing in refuge populations were not present in the Texas populations in 1922. Data presented by Scribner et al. (1992) are not consistent with this hypothesis. They also reported high levels of allelic diversity in native Texas populations; one study site was located in the same drainage basin as Hearne. Most rare alleles in Texas populations of western mosquitofish were retained in populations of mosquitofish that were introduced to Hawaii in 1905 (Scribner et al. 1992). This suggests that allelic diversity was historically high in Texas, and that this diversity was retained in Hawaiian mosquitofish. We conclude that the most parsimonious interpretation of our data is that allelic diversity was reduced during the founding of the Fort Sutter population in 1922.

To further examine the general effects of translocation on genetic variability, we conducted a literature review. Two data bases (M. W. Smith et al. 1982; M. H. Smith et al. 1994) were searched for papers that examined allozyme variation in translocated populations of vertebrates. Although translocated populations are typically defined as only wild populations (Griffith et al. 1989), we also included papers that reported data on the genetic variability for hatchery populations and their respective parental stocks.

In general, genetic diversity was reduced in introduced populations (Table 2). In 50% of the cases we examined, translocated populations had lower heterozygosity than their parental sources (Table 2). In approximately 75% of the cases, refuge populations had reduced levels of allelic diversity. This pattern agrees with theoretical expectations: founding events should have a stronger effect on allelic diversity than on heterozygosity (Nei et al. 1975; Allendorf 1986). Also, reductions in allelic diversity are often due to the loss of rare alleles, which typically have little effect on overall heterozygosity (Allendorf 1986).

Our data and the patterns revealed in the literature suggest that genetic variability is often reduced in refuge populations, and that such reductions typically involve the loss of alleles. In our study all lost alleles were relatively rare (initial frequency less than 0.1), but even rare alleles may be important for the future evolutionary potential of a population (Allendorf 1986). For example, the allele for carbonaria morph in *Biston betularia* apparently existed at very low frequencies (< 0.005) in pre-industrial England (Hartl 1980), but it became common during the industrial period in England (Kettlewell 1973). Although such cases may be rare, they reflect the evolutionary potential of rare alleles.

Retention of rare alleles in translocated populations should be considered an ideal conservation objective. Hedrick et al. (1986) pointed out that real-world constraints may render this goal impractical. They suggested that the cost of retaining rare alleles in small populations often includes selective breeding that can result in reduced heterozygosity. But fish refuge populations can often be maintained at large population sizes. In these cases, undocumented bottlenecks can have important effects on the genetic variability within the population. For species with high reproductive rates such as pupfish (*Cyprinodon sp.*) and various species of *Gambusia*, bottlenecks are not likely to be observed.

This argues for more-intense management and a periodic survey of genetic diversity (Allendorf & Ryman 1987; Quattro & Vrijenhoek 1989). Also, gene flow between refuge populations may serve to restore lost variability (Lacy 1987; Allendorf & Leary 1988). It is noteworthy that hatchery programs that have regularly outcrossed hatchery stock with wild stock did not have reduced levels of genetic variability (Allendorf & Leary 1988; Crozier & Moffett 1989). However, the influence of various migration regimes on the retention of rare alleles awaits further theoretical and empirical examination.

Acknowledgments

We are grateful to the following individuals for sharing their knowledge regarding the historical translocation of western mosquitofish: J. Bonham, J. Combs, R. Coykendall, D. Meyer, B. Paschall, and J. Parker. We thank the following individuals for collecting fish: R. Arias, J. Cavier, D. Meyer, N. Valdez, and M. Warren. We thank L. Woodward and S. Turner for assistance in data collection. We benefitted from discussions with J. Dunham, O. E. Rhodes and D. Sugg. This manuscript was improved by constructive comments from P. Dixon, D. Hernandez-Martich, G. Hoelzer, K. Gubista, S. Jenkins,

K. Kandl, P. Leberg, B. Longland, J. Novak, and an anonymous reviewer. This work was funded by the Biological Resources Research Center at the University of Nevada Reno, a Grant-in-aid of Research from Sigma-Xi to C. A. Stockwell, the Scientific Research Society, a DOE travel grant to C. A. Stockwell and by contract DE-AC09-76SR00819 between the U. S. Department of Energy and the University of Georgia's Savannah River Ecology Laboratory.

Literature Cited

Allendorf, F. W. 1986. Genetic drift and the loss of alleles versus heterozygosity. Zoo Biology **5:**181–190.

Allendorf, F. W., and R. F. Leary. 1986. Heterozygosity and fitness in natural populations of animals. Pages 57–76 in M. Soulé, editor. Conservation biology: The science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.

Allendorf, F. W., and R. F. Leary. 1988. Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout. Conservation Biology **2:**170–184.

Allendorf, F. W., and S. R. Phelps. 1980. Loss of genetic variability in a hatchery stock of cutthroat trout. Transactions of the American Fisheries Society **109:**537–543.

Allendorf, F. W., and N. Ryman. 1987. Genetic management of hatchery stocks. Pages 141–159 in N. Ryman and F. Utter editors. Population genetics & fishery management. Washington Sea Grant, Seattle.

Ammerman, L. K., and D. C. Morizot. 1989. Biochemical genetics of endangered Colorado squawfish populations. Transactions of the American Fisheries Society **118:**435–440.

Ayala, F. J., J. R. Powell, M. L. Tracey, C. A. Mourao, and S. Perez. 1972. Enzyme variability in the *Drosophila willistoni* group. IV. Genetic variation in natural populations of *Drosophila willistoni*. Genetics **70:**113–139.

Baker, A. J., and A. Moeed. 1987. Rapid genetic differentiation and founder effect in colonizing populations of common mynas (*Acridotheres tristis*). Evolution **41:**525–538.

Briscoe, D. A., J. M. Malpica, A. Robertson, G. J. Smith, R. Frankham, R. G. Banks, and J. S. F. Barker. 1992. Rapid loss of genetic variation in large captive populations of *Drosophila* flies: implications for the genetic management of captive populations. Conservation Biology **6:**416–425.

Brown, K. L. 1987. Colonization by mosquitofish (*Gambusia affinis*) of a Great Plains river basin. Copeia **1987:**336–351.

Chesser, R. K., M. W. Smith, and M. H. Smith. 1984. Biochemical genetics of mosquitofish. III. Incidence and significance of multiple insemination. Genetica **64:**77–81.

Cross, T. F., and J. King. 1983. Genetic effects of hatchery rearing in Atlantic salmon. Aquaculture **33:**33–40.

Crozier, W. W., and I. J. J. Moffett. 1989. Amount and distribution of biochemical genetic variation among wild populations and a hatchery stock of Atlantic salmon, *Salmo salar* L., from north-east Ireland. Journal of Fish Biology **35:**665–677.

Echelle, A. A. 1991. Conservation genetics and genetic diversity in freshwater fishes of western North America. Pages 141–153 in W. L. Minckley and J. E. Deacon, editors. Battle against extinction. University of Arizona Press, Tucson.

Edds, D. R., and A. A. Echelle. 1989. Genetic comparisons of hatchery and natural stocks of small endangered fishes: Leon Springs pupfish, Comanche Springs pupfish and Pecos Gambusia. Transactions of the American Fisheries Society **118:**441–446.

Fleischer, R. C., R. N. Williams and A. J. Baker. 1991. Genetic variation within and among populations of the common myna (*Acridotheres tristis*) in Hawaii. Journal of Heredity **82:**205–208.

Gorman, G. C., Y. J. Yang, and S. Y. Yang. 1978. The genetics of colonization: Loss of variability among introduced populations of Anolis lizards (Reptilia: Iguanidae). Journal of Herpetology **12:**47–57.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. Science **245:**477–480.

Hartl, D. L. 1980. Principles of population genetics. Sinauer Associates, Sunderland, Massachusetts.

Hedrick, P. W., P. F. Brussard, F. W. Allendorf, J. A. Beardmore, and S. Orzack. 1986. Protein variation fitness and captive propagation. Zoo Biology **5:**91–99.

Hendrickson, D. A., and J. E. Brooks. 1991. Transplanting short-lived fishes in North American deserts: review, assessment and recommendations. Pages 283–298 in W. L. Minckley and J. E. Deacon, editors. Battle against extinction. University of Arizona Press, Tucson.

Kettlewell, B. 1973. The evolution of melanism. Clarendon Press, Oxford, United Kingdom.

Kolijonen, M. L. 1989. Electrophoretically detectable variation in natural and hatchery stocks of Atlantic salmon in Finland. Hereditas **110:**23–35.

Krumholz, L. A. 1948. Reproduction in the western mosquitofish, *Gambusia affinis affinis* (Baird and Girard) and its uses in mosquito control. Ecological Monographs **18:**1–43.

La Rivers, I. 1962. Fishes and fisheries of Nevada. University of Nevada Press, Reno.

Lacy, R. C. 1987. Loss of genetic diversity from managed populations: interacting effects of drift, mutation, selection and population subdivision. Conservation Biology **1:**143–157.

Lande, R., and G. F. Barrowclough. 1987. Effective population size, genetic variation and their use in population management. Pages 87–123 in M. Soulé, editor. Viable populations for Conservation. Cambridge University Press, New York.

Leberg, P. L. 1990. Influence of genetic variability on population growth: Implications for conservation. Journal of Fish Biology **37** (suppl A):193–195.

Leberg, P. L. 1992. Effects of population bottlenecks on genetic diversity as measured by allozyme electrophoresis. Evolution **46:**477–494.

Leberg, P. L. 1993. Strategies for population reintroduction: Effects of genetic variability on population growth and size. Conservation Biology **7:**194–199.

Lenert, L. G. 1923. *Gambusia affinis*: its use in mosquito control. Weekly bulletin 2. California State Board of Health, Sacramento.

McClenaghan, L., Jr., M. H. Smith, and M. W. Smith. 1985. Biochemical genetics of mosquitofish. IV. Changes in allele frequencies through space and time. Evolution **39:**451–460.

Mitton, J. B., and M. C. Grant. 1984. Associations among protein heterozygosity, growth rate and developmental homeostasis. Annual Review of Ecology and Systematics **15:**479–499.

Nei, M., T. Maruyama, and R. Chakraborty. 1975. The bottleneck effect and genetic variability in populations. Evolution **29:**1–10.

Parkin, D. T., and S. R. Cole. 1985. Genetic differentiation and rates of evolution in some introduced populations of the House Sparrow (*Passer domesticus*) in Australia and New Zealand. Heredity **54:** 15–23.

Quattro, J. M., and R. C. Vrijenhoek. 1989. Fitness differences among remnant populations of the endangered Sonoran topminnow. Science **245:**976–978.

Robbins, L. W., G. D. Hartman, and M. H. Smith. 1987. Dispersal, reproductive strategies and the maintenance of genetic variability in mosquitofish (*Gambusia affinis*). Copeia **1987:**156–164.

Roed, K. H., A. Vold Soldal, and S. Thorisson. 1985. Transferrin variability and founder effect on Iceland reindeer, *Rangifer tarandus* L. Hereditas **103:**161–164.

Ryman, N., and G. Ståhl. 1980. Genetic changes in hatchery stocks of brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Science **37:**82–87.

Scribner, K. T., M. C. Wooten, M. H. Smith, P. K.Kennedy, and O. E.

Rhodes, Jr. 1992. Variation in life history and genetic traits of Hawaiian mosquitofish populations. Journal of Evolutionary Biology **5:**267–288.

Selander, R. K., M. H. Smith, S. Y. Yang, W. E. Johnson, and J. B. Gentry. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old field mouse (*Peromyscus polionotus*). Pages 49–90 in Publication 7102. Studies in Genetics VI. University of Texas, Lubbock.

Smith, M. H., J. D. Hernandez-Martich, J. M. Novak, P. W. Stangel, and J. G. Lowery. 1994. Bibliography of electrophoretic studies of biochemical variation in natural vertebrate populations, vol. 2: 1981-1989. Publication 23. Savannah River Site, National Environmental Research Park, Aiken, South Carolina.

Smith, M. W., C. F. Aquadro, M. H. Smith, R. K. Chesser, and W. J. Etges. 1982. Bibliography of electrophoretic studies of biochemical variation in natural vertebrate populations. Texas Tech Press, Lubbock.

Ståhl, G. 1983. Differences in the amount and distribution of genetic variation between natural populations and hatchery stocks of Atlantic salmon. Aquaculture **33:**23–32.

Sugg, D. W., and R. K. Chesser. 1994. Effective population sizes with multiple paternity.Genetics **137:**1147–1155.

Swofford, D. L., and R. B. Selander. 1981. Biosys-1: A FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. Journal of Heredity **72:**281–283.

Taniguchi, N., K. Suumantadinata, and S. Iyama. 1983. Genetic change in the first and second generations of hatchery stock of black seabream. Aquaculture **35:**309–320.

Taylor, C. E., and G. C. Gorman. 1975. Population genetics of a "colonizing" lizard: natural selection for allozyme morphs in *Anolis grahami*. Heredity **35:**241–247.

Turner, B. J. 1984. Evolutionary genetics of artificial refugium populations of an endangered species, the desert pupfish. Copeia **1984:** 364–369.

Verspoor, E. 1988. Reduced genetic variability in first generation hatchery populations of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Science **45:**1686–1690.

Vrijenhoek, R. C., M. E. Douglas, and G. K. Meffe. 1985. Conservation genetics of endangered fish populations in Arizona. Science **229:** 400–402.

Vuorinen, J. 1984. Reduction of genetic variability in a hatchery stock of brown trout, *Salmo trutta* L. Journal of Fish Biology **24:**339–348.

Williams, J. E., D. W. Sada, C. Deacon-Williams, and other members of the western division of the Endangered Species Committee. 1988. American Fisheries Society guidelines for introduction of threatened and endangered fishes. Fisheries **13:**5–11.

Wright, S. 1931. Evolution in Mendelian populations. Genetics **16:**97–159.